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CONSTANT-RATE STOCKING
OF PREDATOR-PREY SYSTEMS

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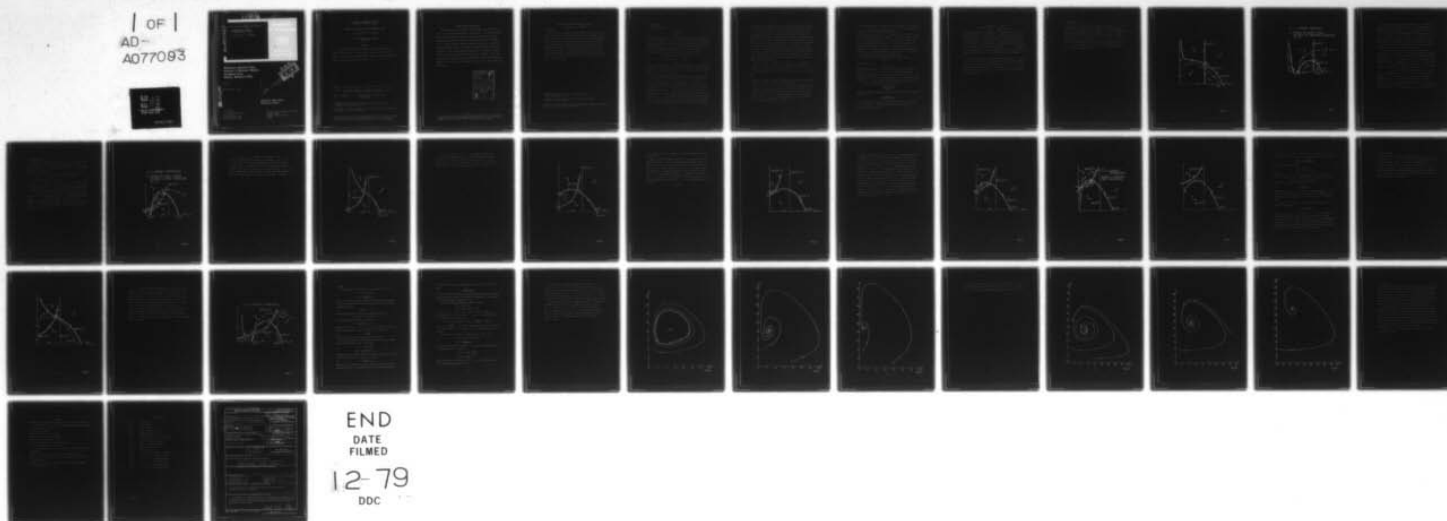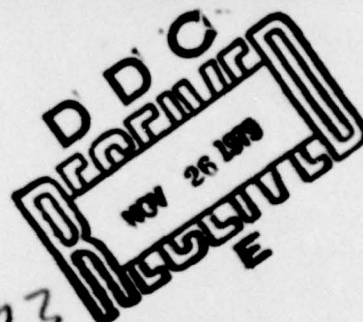
CONSTANT-RATE STOCKING OF PREDATOR-PREY SYSTEMS

F. Brauer[*] and A. C. Soudack[**]

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This report examines →

ABSTRACT

We examine the qualitative effects of constant-rate stocking of
either or both species in a predator-prey system. The hypotheses are
made as mild as possible so that several types of systems with different
qualitative alternatives may be studied. → *(cont on p B)*

AMS (MOS) Subject Classifications - 34C05, 34D35, 69.34, 70.34, 92.00

Key Words - Ecological modelling, predator-prey systems, ordinary
            nonlinear differential equations, stability

Work Unit Numbers 1 and 3 - Applied Analysis and Applications
            of Mathematics

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(cont fr p A)

SIGNIFICANCE AND EXPLANATION

In our previous work on predator-prey systems we have studied the effect of constant-rate harvesting of either species. The same techniques may be used to analyze the effect of negative harvesting rates, which correspond to stocking the system by constant rate addition of members. This is a common practice in many situations, particularly in connection with fish populations where food supply corresponds to prey and fish to predators, and our results indicate some dangers, principally the danger of wiping out the food supply by stocking fish too rapidly. It will be seen that it is safer to increase the food supply. This avoids extinction dangers, tends to stabilize the system, and increases the equilibrium fish population.

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CONSTANT-RATE STOCKING OF PREDATOR-PREY SYSTEMS

F. Brauer[*] and A. C. Soudack[**]

1. INTRODUCTION

In our previous work on predator-prey systems [Brauer and Soudack (1979a), Brauer and Soudack (1979b)] we have studied the effect of constant-rate harvesting of either species. The same techniques may be used to analyze the effect of negative harvesting rates, which correspond to stocking the system by constant rate addition of members. This is a common practice in many situations, particularly in connection with fish populations where food supply corresponds to prey and fish to predators, and our results indicate some dangers, principally the danger of wiping out the food supply by stocking fish too rapidly. It will be seen that it is safer to increase the food supply. This avoids extinction dangers, tends to stabilize the system, and increases the equilibrium fish population.

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2. PRELIMINARIES

We consider the system

(1)
$$x' = xf(x,y) - F$$
$$x' = yg(x,y) - G$$

as a model for the sizes $x(t)$ of a prey population and $y(t)$ of a predator population at time t. The parameters $-F$ and $-G$ are non-negative constants representing rates at which prey and predators respectively are added to the system. We write the stocking rates in this form with $F \leq 0$, $G \leq 0$ in order to make the notation conform to our previous work on harvesting [Brauer and Soudack (1979a), Brauer and Soudack (1979b)].

In order to describe the predator-prey nature of the system, we assume

(2)
$$f_y(x,y) < 0, \quad g_x(x,y) > 0, \quad g_y(x,y) \leq 0$$

for $x > 0$, $y > 0$, and that there exists $J > 0$ such that

(3)
$$g(J,0) = 0$$

In many of the commonly-used models, the function g depends on x only, corresponding to the biological property that the predators do not interfere with one another in their search for prey. In such a model, the curve $g(x,y) = 0$ becomes the vertical straight line $x = J$, and $g(J,y) = 0$ for all $y \geq 0$.

While additional conditions are usually imposed [May (1973), Bulmer (1976)], they are not required for our analysis. Under the conditions (2), (3), every orbit of the system (1) with initial value in the first quadrant of the (x,y) plane at $t = 0$ either leaves the first quadrant in finite time or remains in a bounded subset of the first quadrant for all $t \geq 0$ [Brauer (1979)]. Since $F \leq 0$ and $G \leq 0$, no orbit can leave the first quadrant as t increases; therefore every orbit remains in the first quadrant and the Poincaré-Bendixson theorem is applicable. It follows that every orbit tends as $t \to \infty$ either to a stable equilibrium or to a stable limit cycle. Note, however, that there could be several stable equilibria or limit cycles with different domains of attraction. A stable equilibrium on one of the coordinate axes corresponds

-2-

to extinction of one of the species. This is qualitatively different biologically from

a stable equilibrium in the interior of the first quadrant, corresponding to coexistence

of the two species, even though there may be no qualitative mathematical distinction.

By analyzing the local stability of equilibria, we shall obtain information about the

possible behaviours of orbits, including estimates of the region of asymptotic stability.

We shall ignore the structurally unstable possibility of an equilibrium which is stable

but not asymptotically stable on biological grounds. We shall also not consider further

the possibility of more than one stable limit cycle, or such situations as a stable

equilibrium surrounded by an unstable periodic orbit, which is surrounded by a stable

limit cycle. Such possibilities can occur, and our methods can be adapted to deal with

them, but we avoid them in the interest of simplicity of classification. However, we

shall see that there are situations in which there must be two equilibria, each with a

domain of attraction (see Figure 11).

Since $f_y(x,y) \neq 0$, the equation $f(x,y) = 0$ defines y as a single-valued

function of x, denoted by $y = \phi(x)$, which we may assume non-negative on some

interval $a \leq x \leq K$, with $a \geq 0$ and $K \leq \infty$, and $f(K,0) = 0$ if $K < \infty$. If $a = 0$,

it follows from $f_y(x,y) < 0$ that $f(0,0) \geq 0$, and there exists L, $0 \leq L \leq \infty$, such

that

(4) $f(0,L) = 0$

Biologically, the number L represents the maximum predator density for which the prey

population can establish itself from a small initial population. If $a > 0$ and

$f(a,0) = 0$, then $f(0,0) < 0$; this is the case in which the prey population is unable

to develop even in the absence of predators if it gets too small. The number K is a

carrying capacity for the prey species, the maximum equilibrium population in the

absence of predators. In order to include such examples as the lake eutrophication

model of O'Brien (1974) and the spruce budworm model of Ludwig, Jones, and Holling

(1978), we permit the possibilities $K = \infty$ and $L = \infty$.

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The qualitative behaviour of the system (1) is quite different in the three cases (i) $\alpha > 0$, (ii) $\alpha = 0$ but $L = \infty$, and (iii) $\alpha = 0$, $L < \infty$. Accordingly, it will be necessary to distinguish these cases in what follows.

Since $g_x(x,y) > 0$ and $g_y(x,y) \leq 0$, the equation $g(x,y) = 0$ defines x as a monotone non-decreasing function of y, denoted by $x = \Gamma(y)$. In view of the assumption (2), this function is defined for $0 \leq y < \infty$, and $J = \Gamma(0)$. In many of the models used to describe predator-prey systems, the function g is independent of y, as we have already mentioned. In this case Γ is the constant function $x = J$. Biologically, J is the minimum prey population required for the predator population to establish itself. We will examine explicitly only the case $J < K$; the case $J \geq K$ can be treated in exactly the same way, with analogous results.

An equilibrium of (1) is an intersection $(\hat{x},\hat{y})$ of the prey isocline

(5) $$xf(x,y) - F = 0 ,$$

and the predator isocline

(6) $$yg(x,y) - G = 0 .$$

The assumptions we have made on f and g imply the existence of an equilibrium (x_∞,y_∞) with $x_\infty > 0$, $y_\infty > 0$ for $F = 0$, $G = 0$. We shall assume that this equilibrium, in the interior of the first quadrant, is unique. As F and/or G vary, the equilibrium (x_∞,y_∞) will move, and may disappear for some critical stocking rates. If either F or G is zero, there may also be equilibria on the coordinate axes.

The slope of the prey isocline at an equilibrium $(\hat{x},\hat{y})$ is

$$- \frac{\hat{x}f_x(\hat{x},\hat{y}) + f(\hat{x},\hat{y})}{\hat{x}f_y(\hat{x},\hat{y})} ,$$

which has the same sign as $\hat{x}f_x(\hat{x},\hat{y}) + f(\hat{x},\hat{y})$, by (2), while the slope of the predator isocline is

$$- \frac{\hat{y}g_x(\hat{x},\hat{y})}{\hat{x}g_y(\hat{x},\hat{y}) + g(\hat{x},\hat{y})}$$

which has opposite sign to $\hat{y}g_y(\hat{x},\hat{y}) + g(\hat{x},\hat{y})$ by (2) unless $g(\hat{x},\hat{y}) = 0$ (that is, $G = 0$) and $g_y(\hat{x},\hat{y}) = 0$, in which case the predator isocline is vertical. By examining the coefficient matrix

-4-

$$\Delta(\hat{x}, \hat{y}) = \begin{bmatrix} \hat{x}f_x(\hat{x}, \hat{y}) + f(\hat{x}, \hat{y}) & \hat{x}f_y(\hat{x}, \hat{y}) \\ \hat{y}g_x(\hat{x}, \hat{y}) & \hat{y}g_y(\hat{x}, \hat{y}) + g(\hat{x}, \hat{y}) \end{bmatrix}$$

of the linearized system at an equilibrium $(\hat{x}, \hat{y})$ and observing that $(\hat{x}, \hat{y})$ is a saddle point if and only if $\det \Delta(\hat{x}, \hat{y}) < 0$, it is easy to verify that $(\hat{x}, \hat{y})$ is a saddle point if and only if the slope of the predator isocline is either negative but larger than the slope of the prey isocline or positive but smaller than the slope of the prey isocline. If the predator isocline is vertical, $(\hat{x}, \hat{y})$ can not be a saddle point. This generalizes a criterion of Bulmer (1976) for $F = 0$, $G = 0$. In particular, the remark of Bulmer that if there is a unique equilibrium in the interior of the first quadrant, then this equilibrium can not be a saddle point, extends to arbitrary F and G.

In the following sections, we shall examine the effect of varying F, or G, or both F and G simultaneously. We shall pay particular attention to the mathematical catastrophes which may arise if the equilibrium which is at (x_∞, y_∞) for $F = G = 0$ coalesces with the equilibrium which is at the origin for $F = G = 0$. There is another saddle point which is at $(K, 0)$ for $F = G = 0$, but we shall see that it plays no role in the analysis when $F < 0$ or $G < 0$.

3. PREY STOCKING

We fix $G = 0$ and decrease F from zero. If $\alpha = 0$, then for $F = 0$ there is an equilibrium (x_∞, y_∞) which is not a saddle point and there are two saddle points $S_1(0,0)$ and $S_2(K,0)$. If $\alpha > 0$, then for $F = 0$, S_1 is an asymptotically stable equilibrium, and there is a second saddle point $S_3(\alpha,0)$. As F decreases, the prey isocline moves up, since $f_y(x,y) < 0$. For $F < 0$ the prey isocline is asymptotic to the y-axis and to the curve $f(x,y) = 0$. Thus if $\alpha = 0$, S_1 moves into the second quadrant and S_2 moves to the right along the x-axis (Figure 1). If $\alpha > 0$, S_1 moves to the right and S_3 moves to the left along the x-axis until S_1 and S_3 coalesce and disappear (Figure 2).
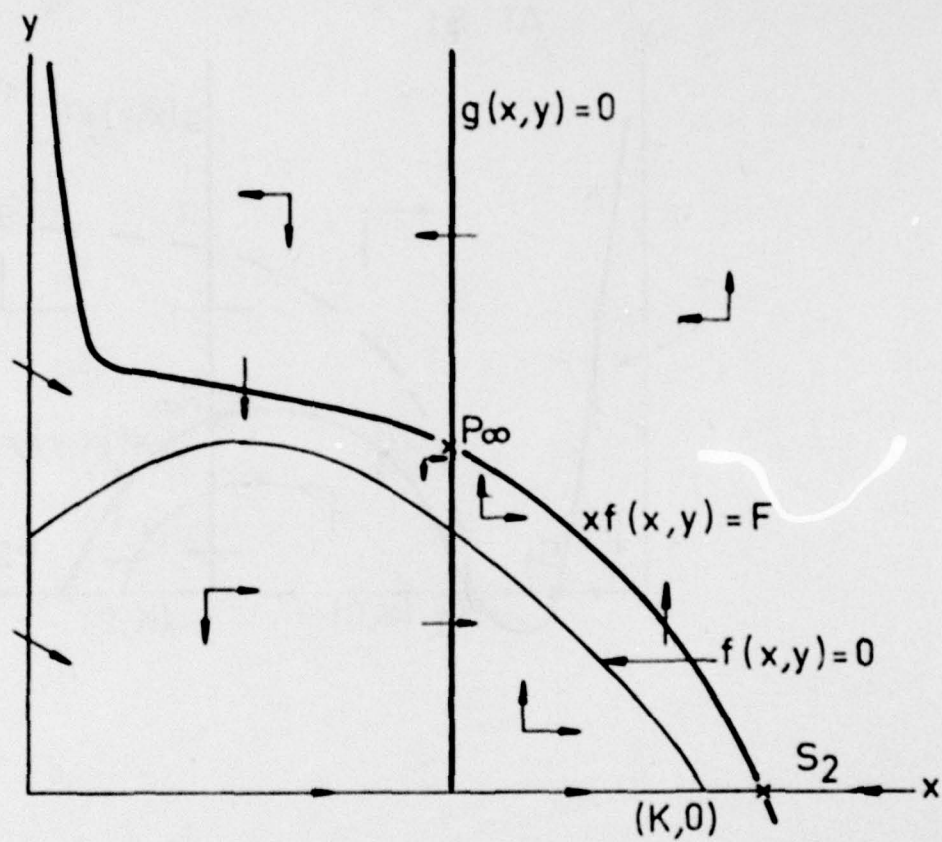
Fig. 1

- - - SADDLE ASYMPTOTE

U REGION OF INITIAL STATES
LEADING TO PREDATOR EXTINCTION
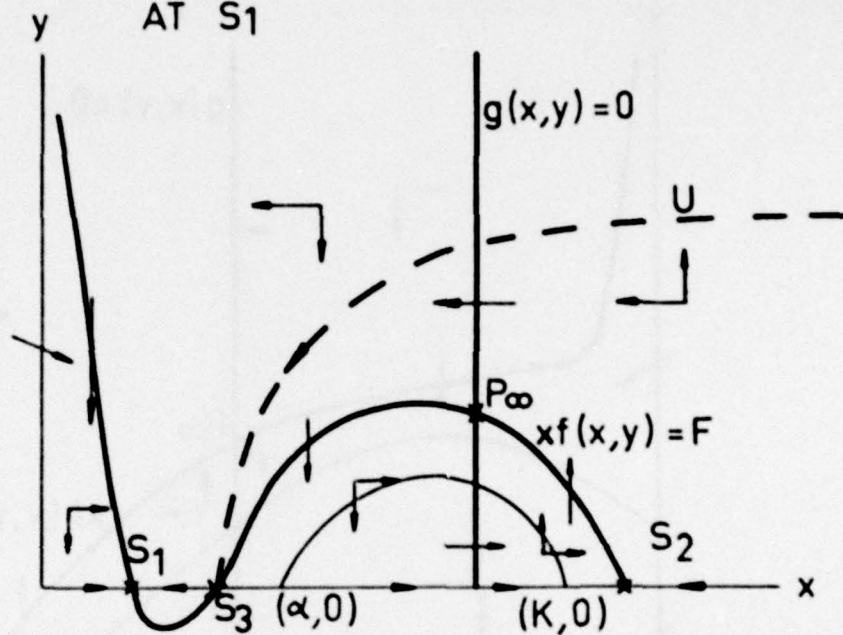AT S_1

-8-

Fig. 2

Since every orbit which starts in the first quadrant at $t = 0$ remains in a bounded subset of the first quadrant for all $t \geq 0$, the Poincaré-Bendixson theorem shows that every orbit tends either to P_- or to a limit cycle around P_-, or to S_1 (if $a > 0$) as $t \to \infty$, with the exception of orbits starting on the x-axis and tending to the saddle point S_2 and, in the case $a > 0$, a separatrix in the first quadrant tending to the saddle point S_3 (Figure 2). In the case $a > 0$ this separatrix divides the first quadrant into two regions, the domain of attraction of P_- or a limit cycle around P_-, for which both species coexist, and the domain of attraction of S_1, for which the predators become extinct as $t \to \infty$.

As F decreases, the equilibrium P_- moves up along the curve $g(x,y) = 0$. If $xf_x(x,y) + f(x,y) < 0$ for large y, as is the case for the commonly used predator-prey models, then it is easy to see that the equilibrium P_- must be asymptotically stable for all large $|F|$. This suggests that if $a = 0$ there are essentially two possibilities. Either P_- is asymptotically stable for all $F \leq 0$ and all orbits tend to P_-, or P_- is unstable initially and orbits tend to a limit cycle around P_- but as $|F|$ increases, P_- stabilizes and orbits tend to P_-.

If $a > 0$, the behaviour in the domain of attraction of P_- or a limit cycle around P_- is the same as for the case $a = 0$. As $|F|$ increases, the domain of attraction of S_1 shrinks until S_1 and S_3 coalesce. This coalescence is a mathematical catastrophe, though without the usual connotation of disaster. It signals a transition to a qualitative picture like the case for $a = 0$ with no possibility of predator extinction; there exists $F_c < 0$ with predator extinction for some initial states if $0 \geq F > F_c$ and coexistence for all initial states if $F < F_c$.

4. PREDATOR STOCKING

We now fix $F = 0$ and decrease G from zero. For $G < 0$, the predator isocline
(6) is asymptotic to the curve $g(x,y) = 0$ as $y \to \infty$ and lies to the left of
$g(x,y) = 0$ because of (2). In order to analyze the behaviour as G decreases we must
separate the three possibilities:

(a) $a > 0$ so that the curve $f(x,y) = 0$ does not intersect the positive y-axis

(b) $a = 0$ but $L = \infty$, so that $f(0,y) > 0$ for $y > 0$ and $\lim_{x \to 0_+} \Phi(x) = +\infty$.

(c) $a = 0$ and there exists $L < \infty$ with $f(0,L) = 0$.

If $a > 0$, as G decreases P_∞ moves along $f(x,y) = 0$ to the left, S_1 moves
up the y-axis, and S_3 moves along $f(x,y) = 0$ to the right, while S_2 moves down
into the fourth quadrant (Figure 3). Just as in the prey stocking situation, there
is a separatrix at S_3 which divides the first quadrant into a domain of attraction
of P_∞ or a limit cycle around P_∞ for which both species coexist, and a domain of
attraction of S_1. The only difference is that now S_1 corresponds to prey extinction.
Eventually, S_3 and P_∞ coalesce and disappear. When this occurs, we have a
mathematical catastrophe, and all orbits tend to S_1 (prey extinction). Thus there
exists $G_c < 0$ with coexistence for some initial states if $0 \geq G > G_c$ and prey
extinction for all initial states if $G < G_c$.

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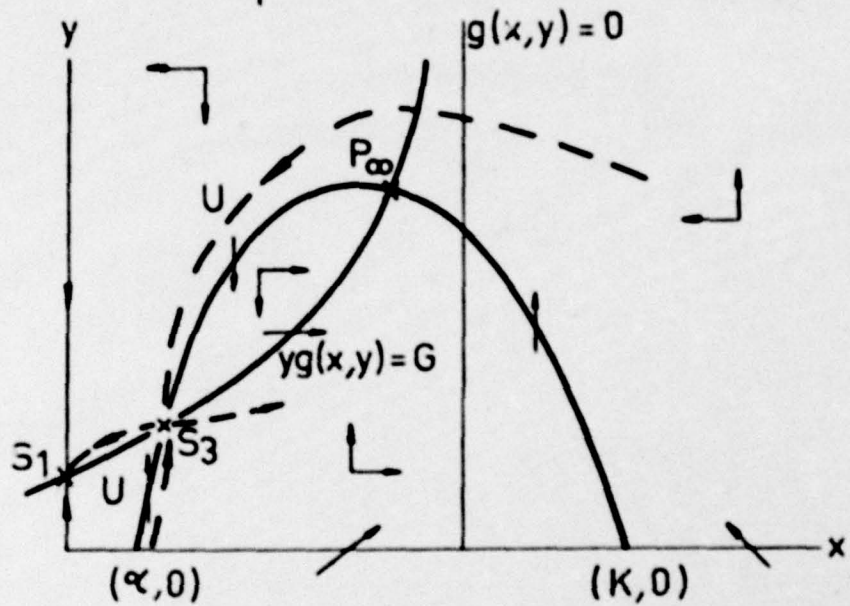
U REGION OF INITIAL STATES LEADING TO PREY EXTINCTION AT S_1

-11-

Fig. 3

If $a = 0$ but $L = \infty$, as G decreases P_- moves along $f(x,y) = 0$ to the left and S_1 moves up the y-axis (Figure 4). For such models, $f_x(x,y) < 0$, and it is easy to verify that this implies the asymptotic stability of the equilibrium P_- . Since $f(x,y) = 0$ never meets the y-axis, there is no coalescence, and every orbit with initial value in the interior of the first quadrant tends to P_- as $t \to \infty$. As $|G|$ becomes large, P_- comes very close to the y-axis, and a small perturbation may wipe out the prey population. In practical terms, the system is not stable.

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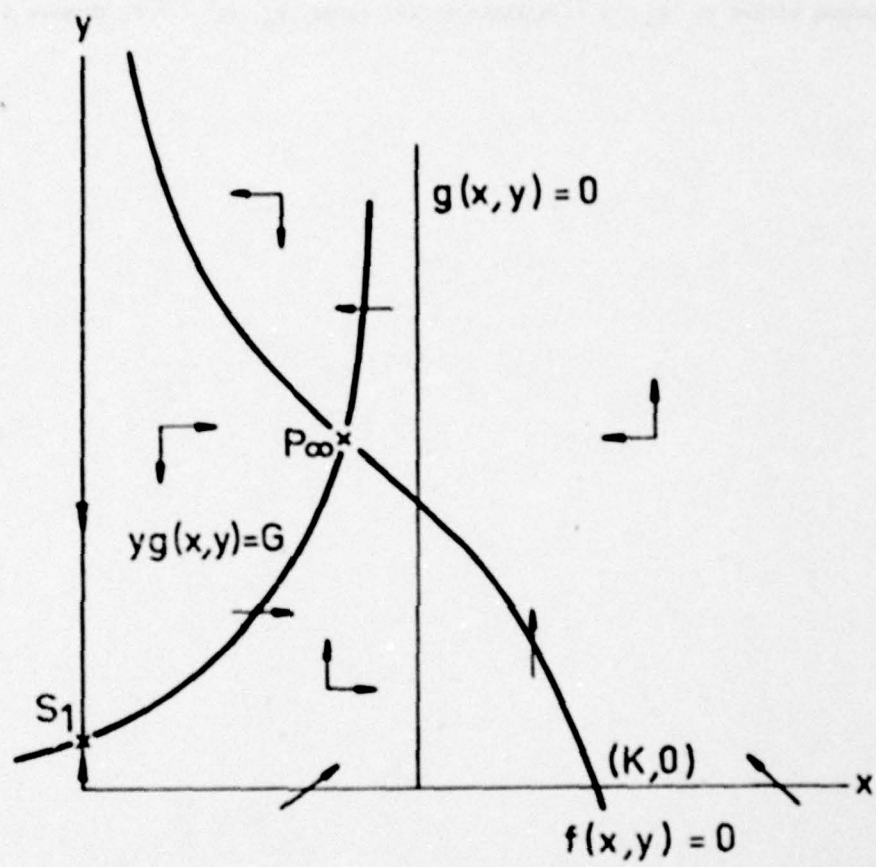
Fig. 4

The situation in which $a = 0$ and $L < \infty$ is considerably more complicated. Since this is the one which describes most of the commonly used models, we examine it in detail. As G decreases, P_∞ moves to the left along $f(x,y) = 0$ and S_1 moves up the y-axis, with every orbit starting in the interior of the first quadrant tending either to P_∞ or to a limit cycle around P_∞ as $t \to \infty$ (Figure 5).
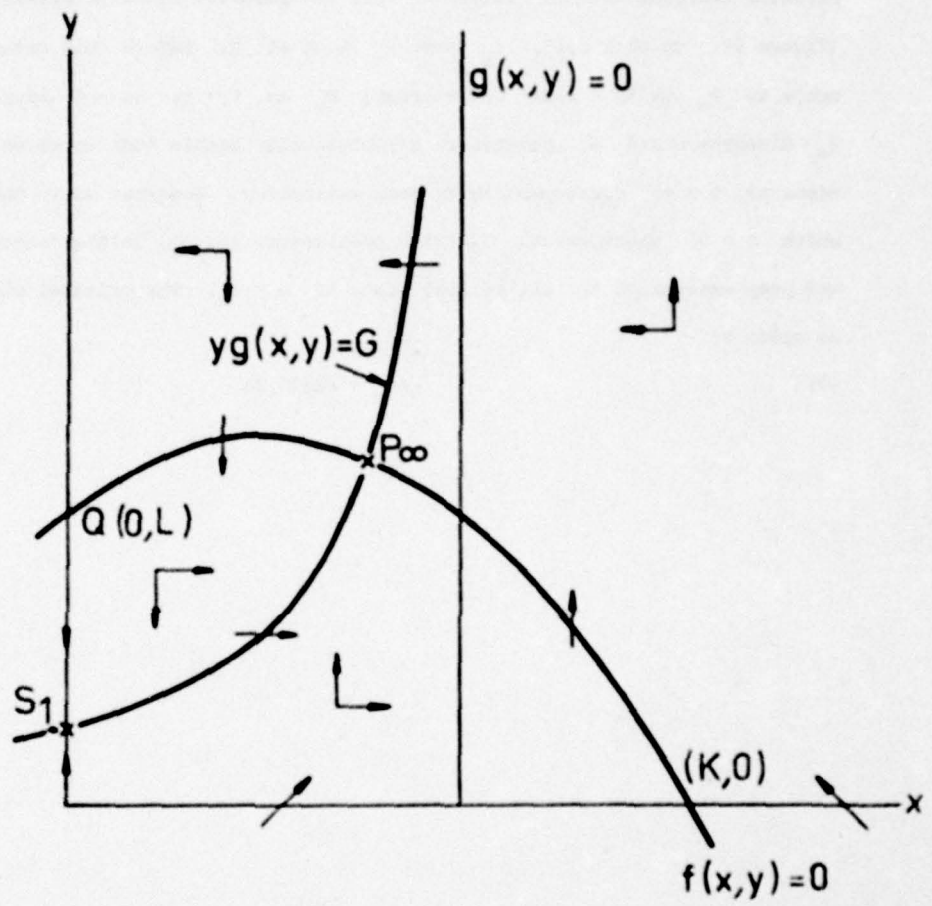
-15-

Fig. 5

As S_1 reaches the Point $Q(0,L)$ where $f(x,y) = 0$ meets the y-axis, there are two possible cases:

Case I: The slope of the prey isocline for $P = 0$ is less than the slope of the predator isocline with G chosen so that the predator isocline passes through $(0,L)$ (Figure 6). In this case, S_1 and P_- meet at Q. Before this occurs, every orbit tends to P_- or to a limit cycle around P_- as $t \to \infty$. As $-G$ increases further, P_- disappears and S_1 becomes an asymptotically stable node to which every orbit tends as $t \to \infty$, corresponding to prey extinction. Somewhat as in the situation in which $a > 0$, there exists G_c with coexistence for all initial states if $0 \geq G > G_c$ and prey extinction for all initial state if $G < G_c$. The critical stocking rate $-G_c$ is given by

$$(7) \qquad\qquad -G_c = -Lg(0,L)$$

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$yg(x,y) = G$

$g(x,y) = 0$

Q $\times$ P_∞
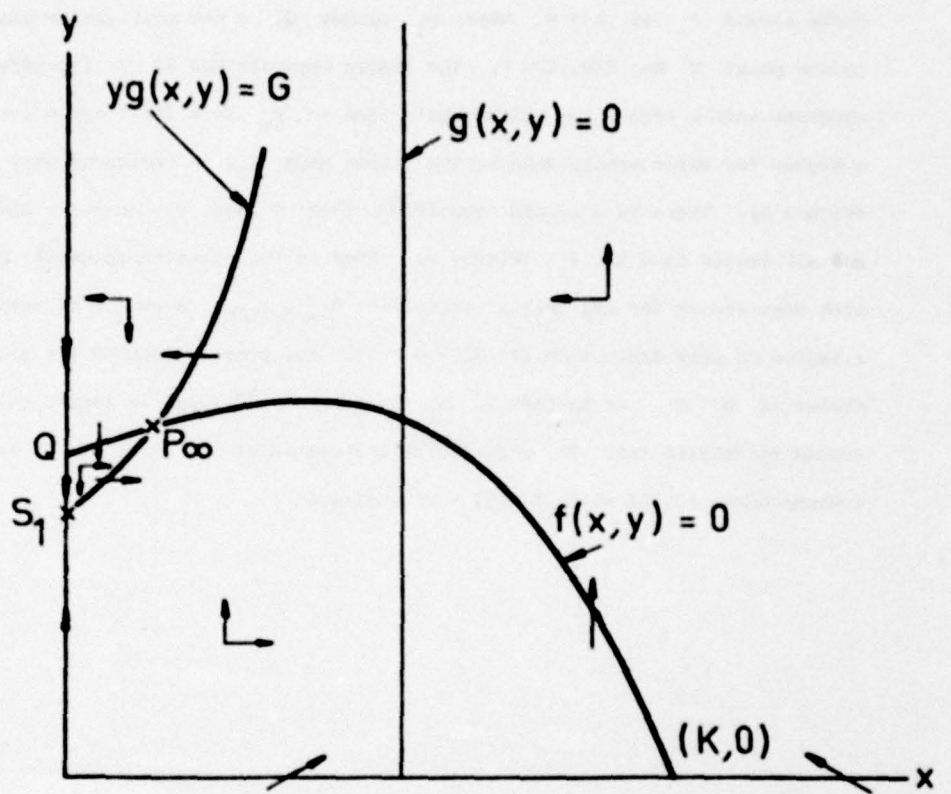
S_1

$f(x,y) = 0$

$(K,0)$

-17-

Fig. 6

Case II: The slope of the prey isocline for $F = 0$ is greater than the slope of the predator isocline with G chosen so that the predator isocline passes through $(0, L)$ (Figure 7). In this case S_1 reaches Q while P_∞ is still in the interior of the first quadrant. Until this occurs, every orbit tends to P_∞ or to a limit cycle around P_∞ as $t \to \infty$. When S_1 passes Q, a new equilibrium appears - a saddle point T on $f(x,y) = 0$. The stable separatrices at T separate the first quadrant into a region for which orbits tend to P_∞ or a limit cycle around P_∞ and a region for which orbits tend to the stable node S_1, a region of prey extinction (Figure 8). There is a second transition, when T and P_∞ coalesce and disappear, and all orbits tend to S_1 (Figure 9). Thus in this case there exist G_c, $G^* < 0$ with coexistence for all initial states if $0 \geq G > G_c$, a region of coexistence and a region of prey extinction if $G_c > G > G^*$, and prey extinction for all initial states if $G < G^*$. As in Case 1, G_c is given by (7), and is easily calculated. The second transition rate G^* can also be calculated as the value of G for which the intersections of (6) with $f(x,y) = 0$ coalesce.
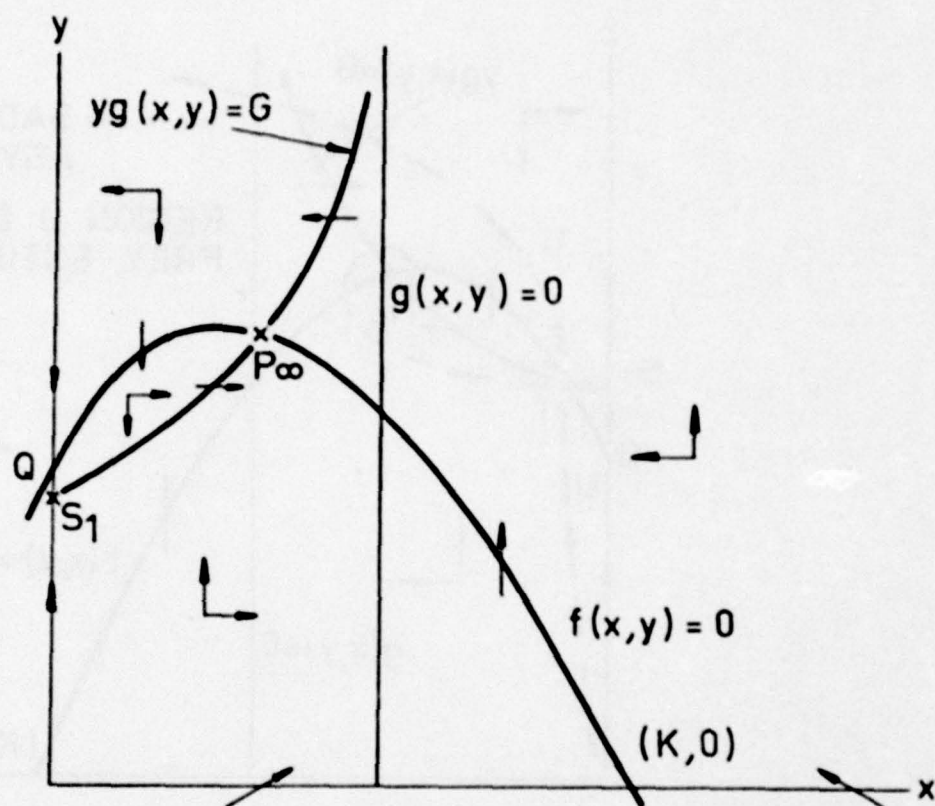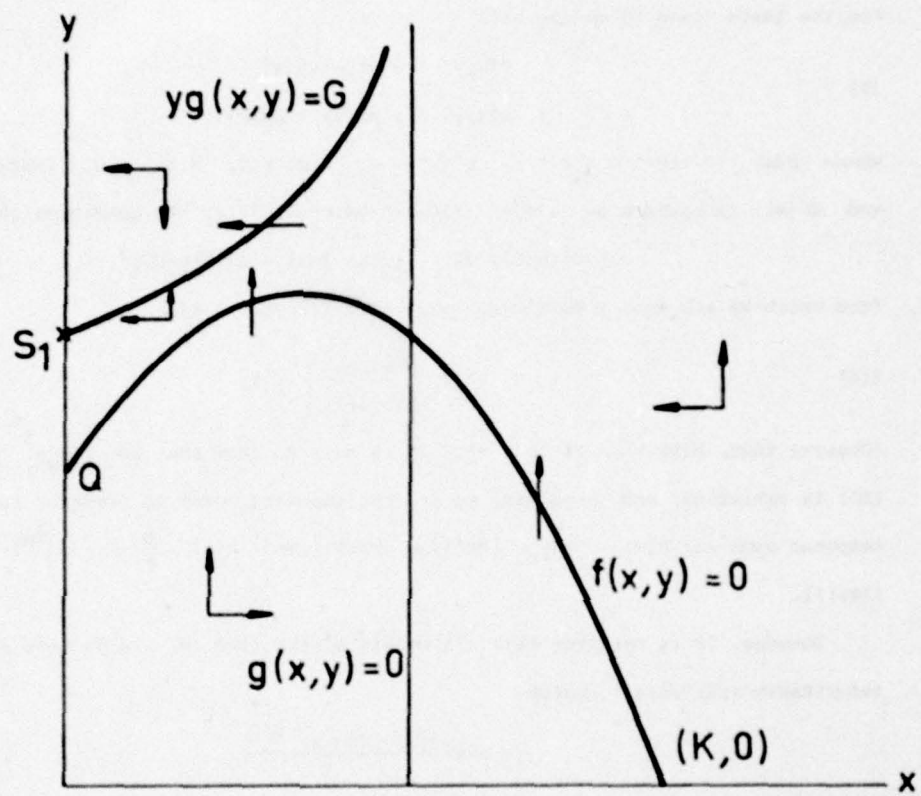
Fig. 7

Fig. 8

Fig 9

Since the distinction between Cases I and II is in terms of the slopes of the isoclines at $(0,L)$, it is easy to see that the system (1) is in Case I if and only if

$$(8) \qquad -\frac{f_x(0,L)}{f_y(0,L)} < -\frac{Lg_x(0,L)}{g(0,L) + Lg_y(0,L)}$$

For the large class of models with

$$(9) \qquad \begin{aligned} f(x,y) &= \phi(x) - yh(x) \\ g(x,y) &= s[xh(x) - Jh(J)] \end{aligned}$$

where $\phi(x) \geq 0$ for $0 \leq x \leq K$, $\phi'(x) \leq 0$, $h(x) \geq 0$, $h'(x) \leq 0$, $[xh(x)]' > 0$, and $xh(x)$ is bounded as $x \to \infty$ [Maynard Smith (1974)], the condition (8) reduces to

$$Jh(J)[h(0)\phi'(0) - \phi(0)h'(0)] < \phi(0)[h(0)]^2 ,$$

from which we see that a sufficient condition for Case I is

$$(10) \qquad Jh(J)\left|\frac{-h'(0)}{[h(0)]^2}\right| \leq 1$$

(Observe that $h(0) > 0$ if $L < \infty$). It is easy to show that if $\left|\frac{1}{h(x)}\right|'' \geq 0$, then (10) is satisfied, and therefore, so are the standard forms of predator functional response such as $h(x) = \frac{1}{x + \lambda}$ [Holling (1965)] and $h(x) = \frac{b}{x}(1 - e^{-cx})$ [Ivlev (1961)].

However, it is not true that all models of the form (9) are in Case I. The (admittedly artificial) choice

$$h(x) = \frac{1 - (1 + x)^{-1/2}}{x} ,$$

for which $h(0) = \frac{1}{2}$, $h'(0) = -\frac{3}{8}$, violates (10) if $J > 8$. More significantly, in Section 6 we shall describe a class of predator-prey models in which predators interfere with one another for which the system (1) is in Case II if this interference is large enough. Thus the biological effect of predator interference is to give a possibility of prey survival (depending on the initial state) under predator stocking which would guarantee prey extinction without this interference.

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5. TWO-SPECIES STOCKING

Simultaneous stocking of both species corresponds to making both F and G different from zero. If $a = 0$, then S_1 moves into the second quadrant and S_2 moves into the fourth quadrant. There is no possibility of catastrophe and for all $F < 0$, $G < 0$ every orbit tends either to P_∞ or to a limit cycle around P_∞ as $t \to \infty$. Qualitatively, the situation is similar to predator stocking when $L = \infty$ (Figure 10). For large stocking rates the equilibrium becomes asymptotically stable but there is a practical instability since the equilibrium comes very close to the y-axis and a small perturbation may wipe out the prey population.
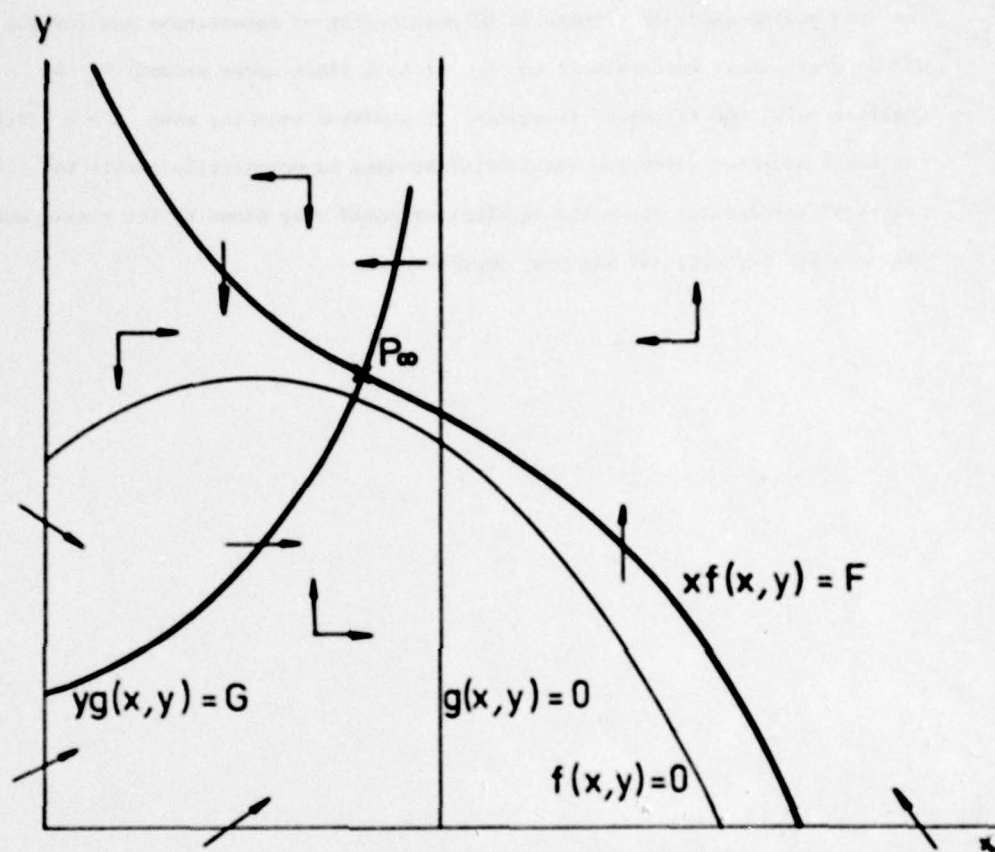
Fig. 10

If $\alpha > 0$, the situation is slightly different when $-F$ is smaller than the stocking rate for which S_1 and S_3 coalesce (Figure 11). There are two coexistence regions divided by the stable separatrices tending to the saddle point S_3. One is the domain of attraction of P_- or a limit cycle around P_-, and the other is the domain of attraction of the asymptotically stable equilibrium S_1, which is in the interior of the first quadrant. The coexistence region is the entire first quadrant, but there are two possible equilibria, depending on the initial state.

There are many practical questions which can be raised for two-species stocking problems. For example, what is the effect of increasing one stocking rate while holding the other fixed? Such questions may be studies most readily by a computer simulation. In the following section, we shall indicate the results of some simulations for a class of examples.

- - - - SADDLE ASYMPTOTES
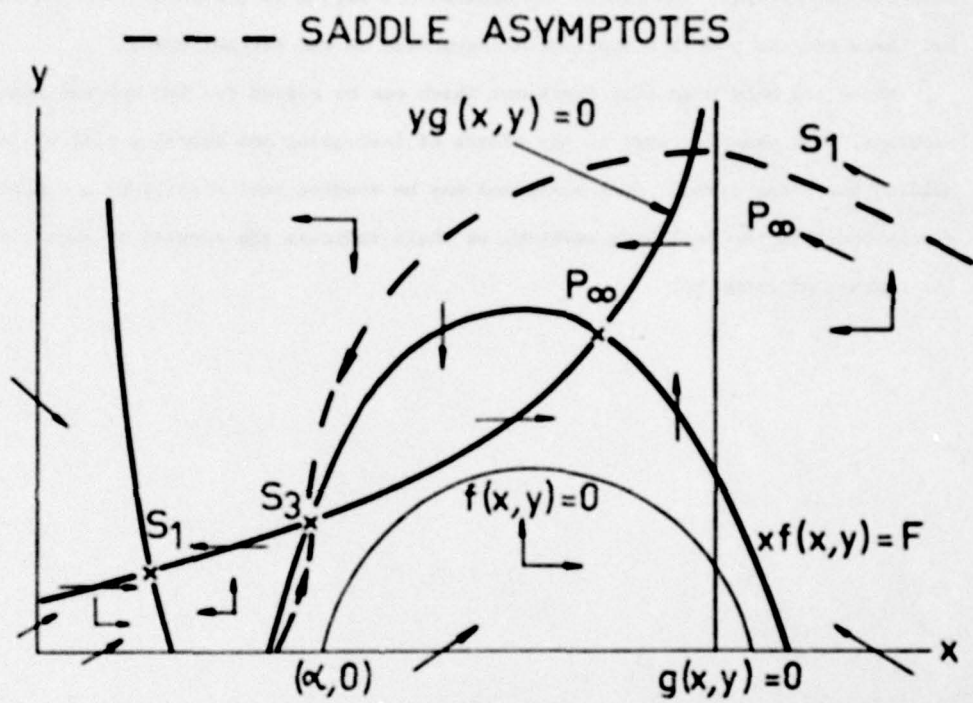
Fig. 11

6. EXAMPLES

One commonly used model for predator-prey interactions [Holling (1965)] is

(11)
$$f(x,y) = r\left(1 - \frac{x}{K}\right) - \frac{y}{x + A}$$

$$g(x,y) = \frac{sA(x - J)}{(x + A)(J + A)}$$

It may easily be deduced from our earlier studies on harvesting [Brauer and Soudack (1979a), Brauer and Soudack (1979b)] that under pure prey stocking, the equilibrium is asymptotically stable if

$$-F > \frac{rJ^2}{KA} (K - A - 2J) .$$

Under pure predator stocking, the equilibrium is asymptotically stable if

$$rx_\infty (J + A)(2x_\infty + A - K) + sAK(J - x_\infty) > 0 ;$$

the corresponding stocking rate may be calculated from

$$-G = \frac{rsA}{K(J + A)} (J - x_\infty)(K - x_\infty)$$

This model is of the type $\alpha = 0$, $L < \infty$, with $L = rA$. The predator stocking rate for which the saddle point S_1 reaches the point $Q(0,L)$ is given by

(12)
$$-G_c = \frac{rsAJ}{J + A}$$

As we have shown in Section 4, this model is necessarily in Class I.

A variant of the model (11) which incorporates interference among the predators has been suggested by Bazykin (1974). For this model

(13)
$$f(x,y) = r\left(1 - \frac{x}{K}\right) - \frac{y}{x + A}$$

$$g(x,y) = \frac{sA(x - J)}{(x + A)(J + A)} - \mu y$$

he parameter μ may be viewed as a measure of the amount of interference. This model is also of the type $\alpha = 0$, $L < \infty$ with $L = rA$, but now

(14)
$$-G_c = \frac{rsJA}{J + A} + \mu r^2 A^2$$

Comparison with (12) shows that for this model a higher rate of predator stocking is needed before a transition is reached than when there is no predator interference.

By examining the condition (8), we observe that the model (13) is in Case I if and only if

$$(15) \qquad \mu < \frac{s(K + J)}{2r(K - A)(J + A)}$$

Thus there is a predator stocking range in which either both species coexist or the prey species becomes extinct, depending on the initial state, whenever there is enough interference among the predators in searching for prey.

This principle generalizes immediately to models of the form

$$f(x,y) = \phi(x) - yh(x)$$

$$g(x,y) = s[xh(x) - Jh(J)] - \mu a(y) ,$$

with $\phi(x) \geq 0$ for $0 \leq x \leq K$, $\phi'(x) \leq 0$, $h(x) \geq 0$, $h'(x) \leq 0$, $[xh(x)]' > 0$, $xh(x)$ bounded as $x \to \infty$, $a(0) = 0$, $a'(y) > 0$, $a'(0) = 1$. It is easy to see that such a model is in Case I if and only if

$$[\phi'(0)h(0) - \phi(0)h'(0)][sJh(J) + \mu\{a(L) + a'(L) \frac{\phi(0)}{h(0)}\}] < s\phi(0)[h(0)]^2$$

Since $a(L) + a'(L) \frac{\phi(0)}{h(0)} > 0$, this condition can be violated by taking μ sufficiently large. Thus the model (13) is of the type $a = 0$, $L < \infty$, and may be either Case I or Case II.

Another variant of (11), based on a suggestion of Clark (1976), p. 166, is

$$(16) \qquad f(x,y) = r(x - a)(1 - \frac{x}{K}) - \frac{y}{x + A}$$

$$g(x,y) = \frac{sA(x - J)}{(x + A)(J + A)}$$

It is easy to see that this is of the type $a > 0$. The spruce budworm model of Ludwig, Jones, and Holling (1978) is of the form

$$f(x,y) = r(1 - \frac{x}{K}) - \frac{\beta x}{a^2 + x^2}$$

$$g(x,y) = s(1 - \frac{y}{Mx})$$

which is easily seen to be of the type $a = 0$, $L = \infty$. Thus all the types of model we have considered are realizable in practice.

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We have performed some computer simulations for the model (11) with $r = 1$, $s = 1$, $K = 40$, $J = 10$, $A = 10$. It is easy to calculate that the equilibrium (x_∞, y_∞) is asymptotically stable under pure prey stocking if and only if $-F > 2.50$ and under pure predator stocking if and only if $-G > 2.1875$. Further, $-G_c = 5.00$, and the variant (13) with the same parameters is in Case II for $\mu > \frac{1}{24}$. If $\mu = 0.05$, then $-G_c = 10.00$ for (13). These results can of course be confirmed by computer simulation.

Computer simulation is more useful in examing the behaviour of the system under simultaneous stocking of both species. For example, under fixed prey stocking, $-F = 1$, we found that for $-G = 0.5$ there is a limit cycle, which becomes an asymptotically stable spiral point for $-G = 3$, and an asymptotically stable node for $-G = 6$. However, as $-G$ increases, the equilibrium approaches the y-axis, raising the possibility of prey extinction caused by a small perturbation (Figures 12, 13, 14).
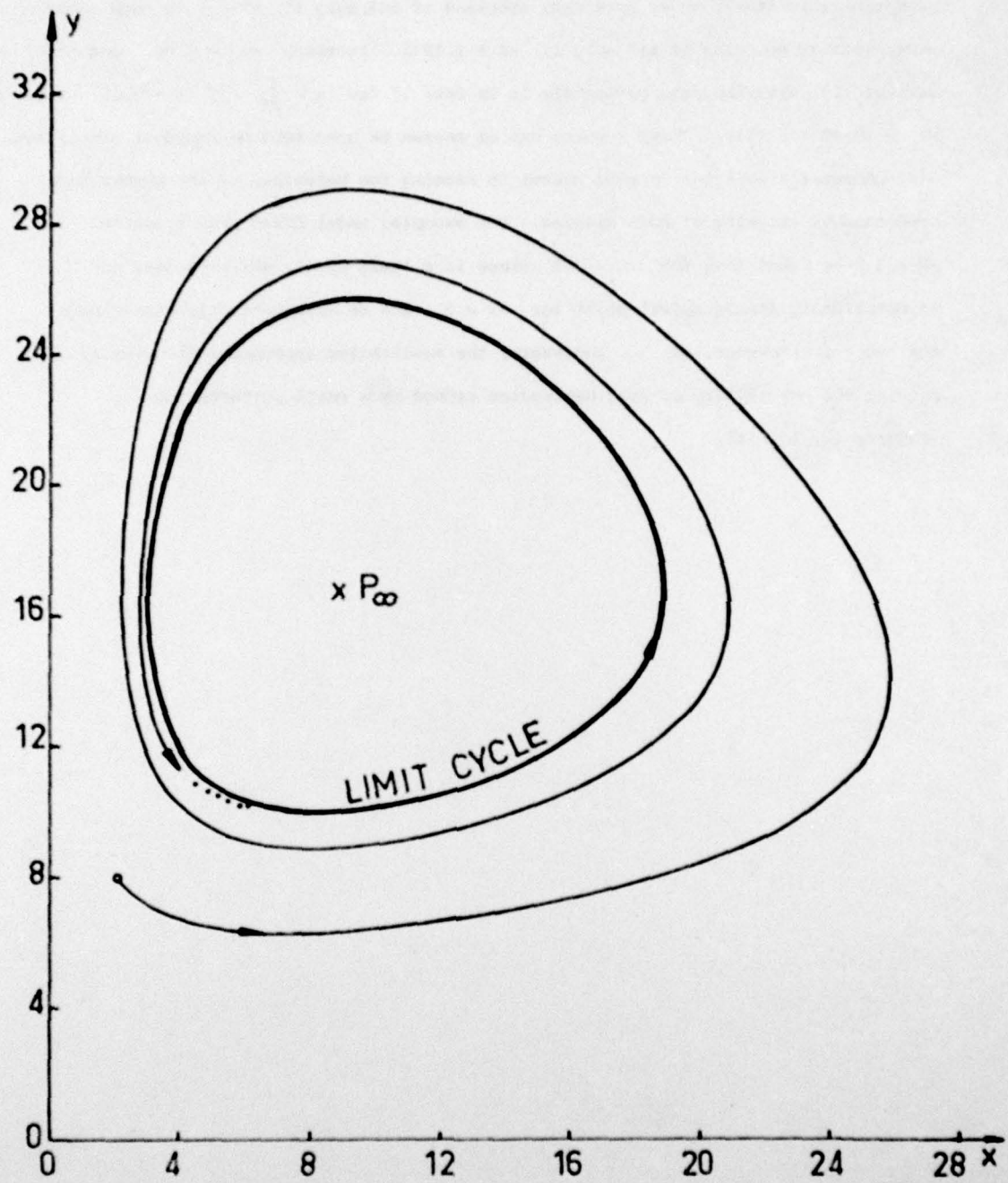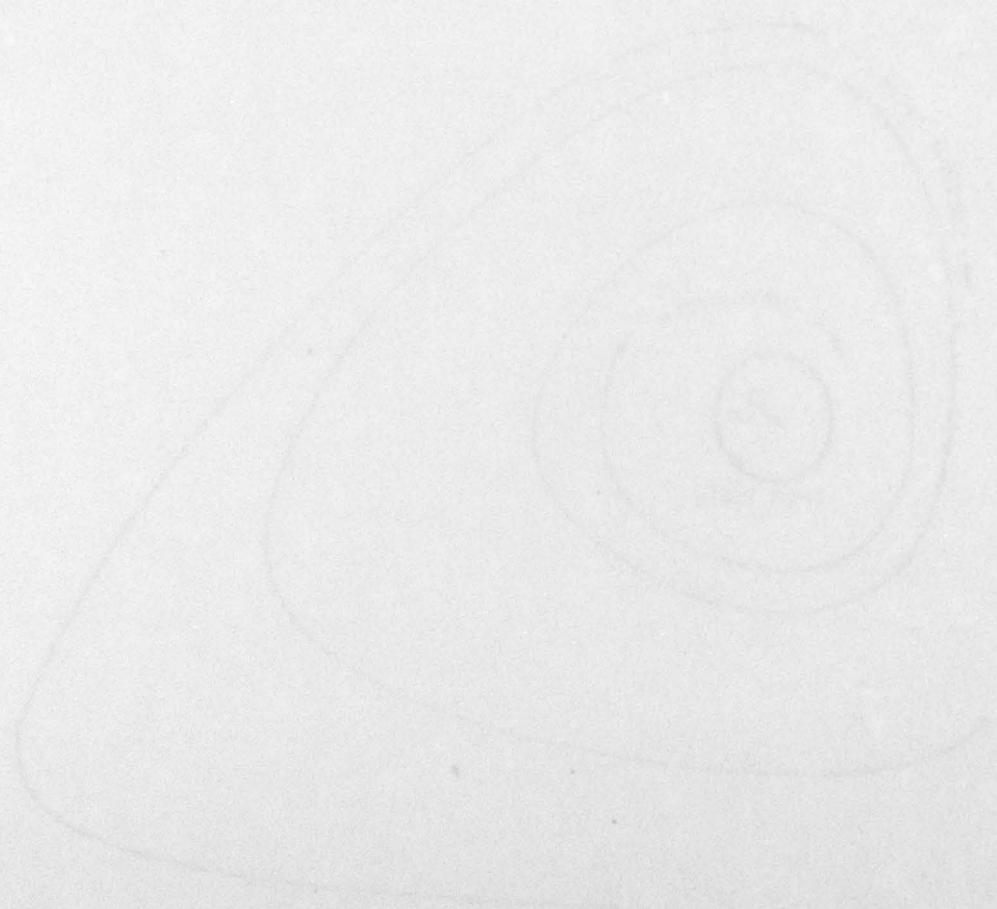
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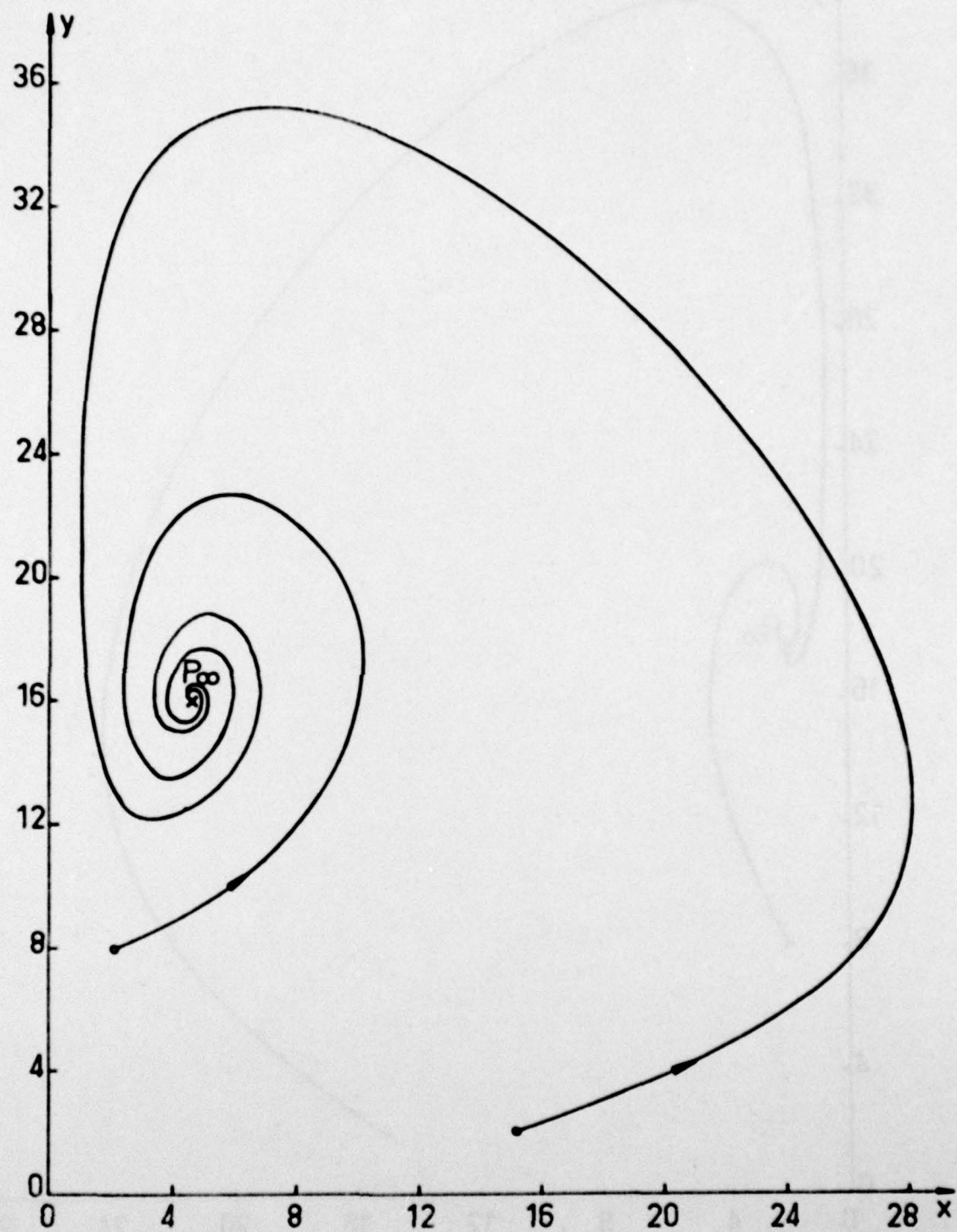
Fig. 13
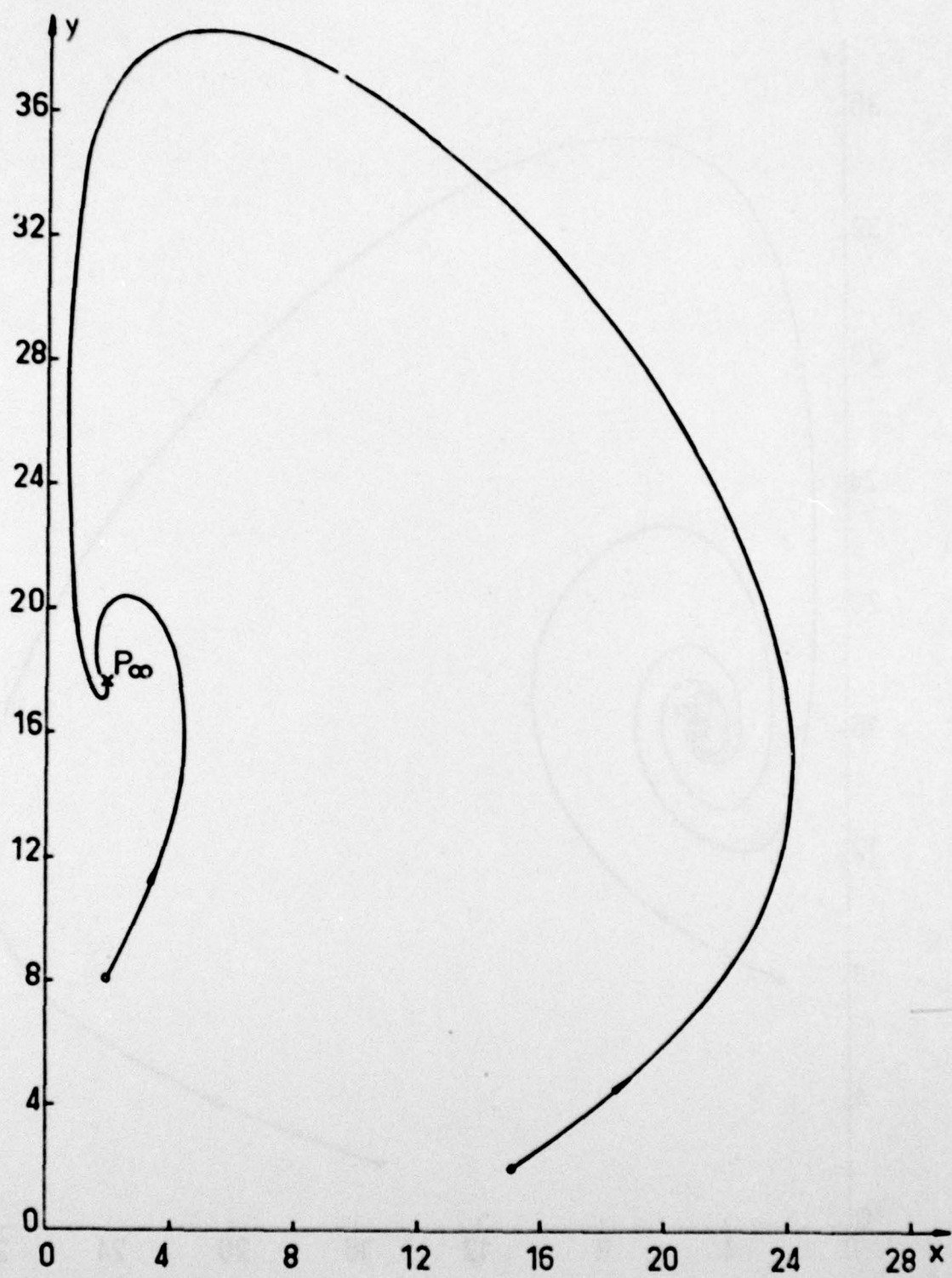
Fig.14

Under fixed predator stocking, $-G = 0.5$, we found that for $-F = 2$ there is a limit cycle, considerably smaller than the one for $-F = 1$. For $-F = 4$ and for $-F = 8$, the equilibrium is an asymptotically stable spiral point (Figures (15, 16, 17).
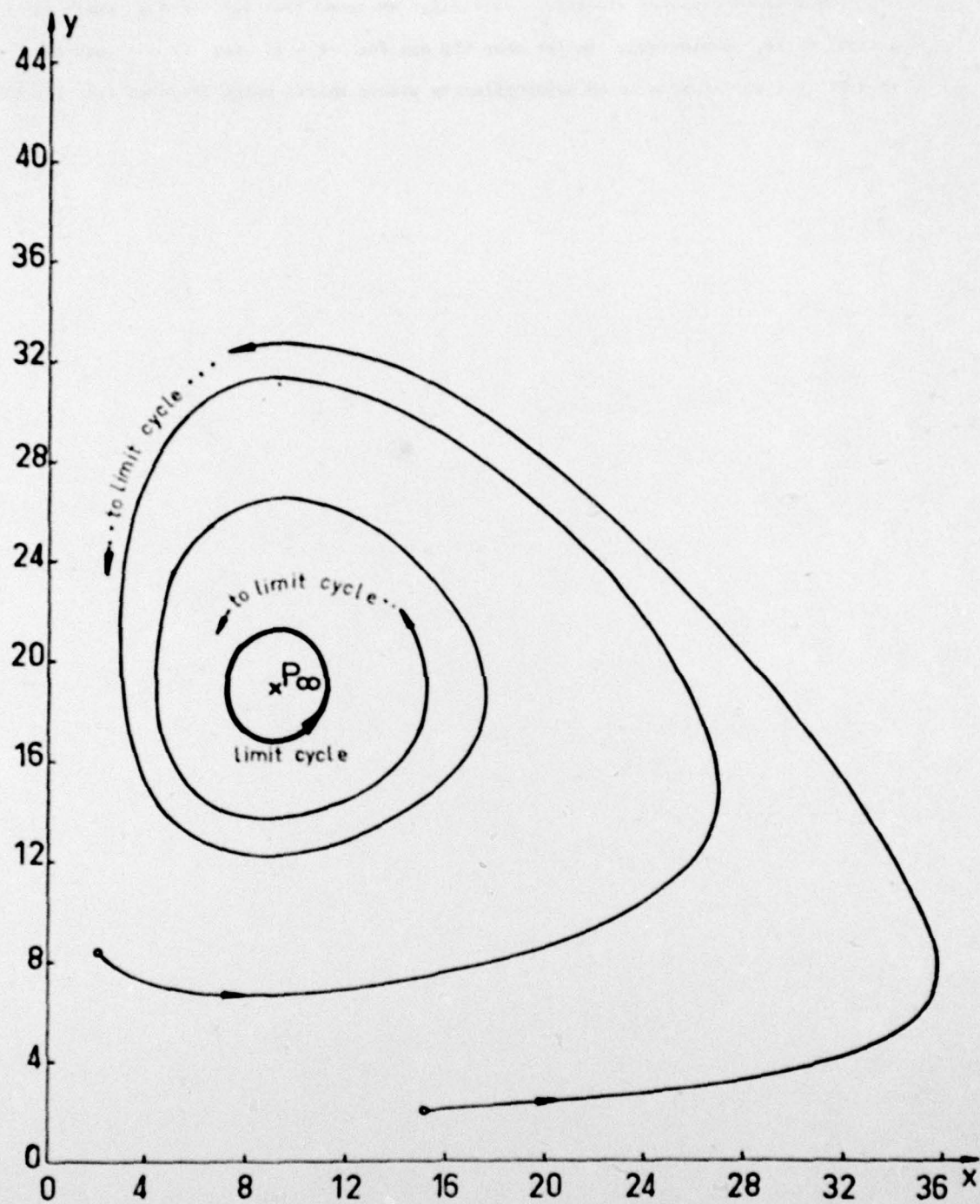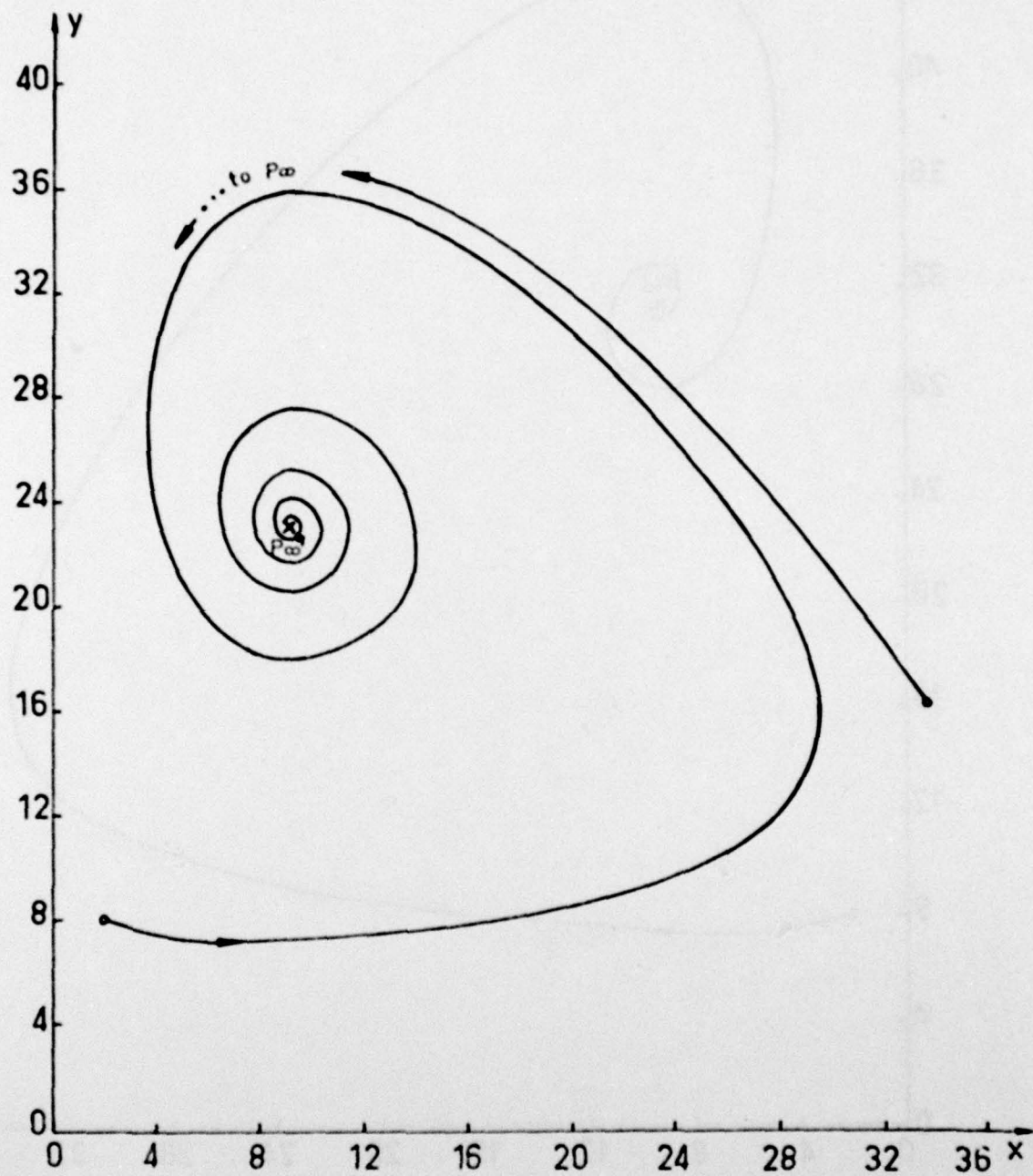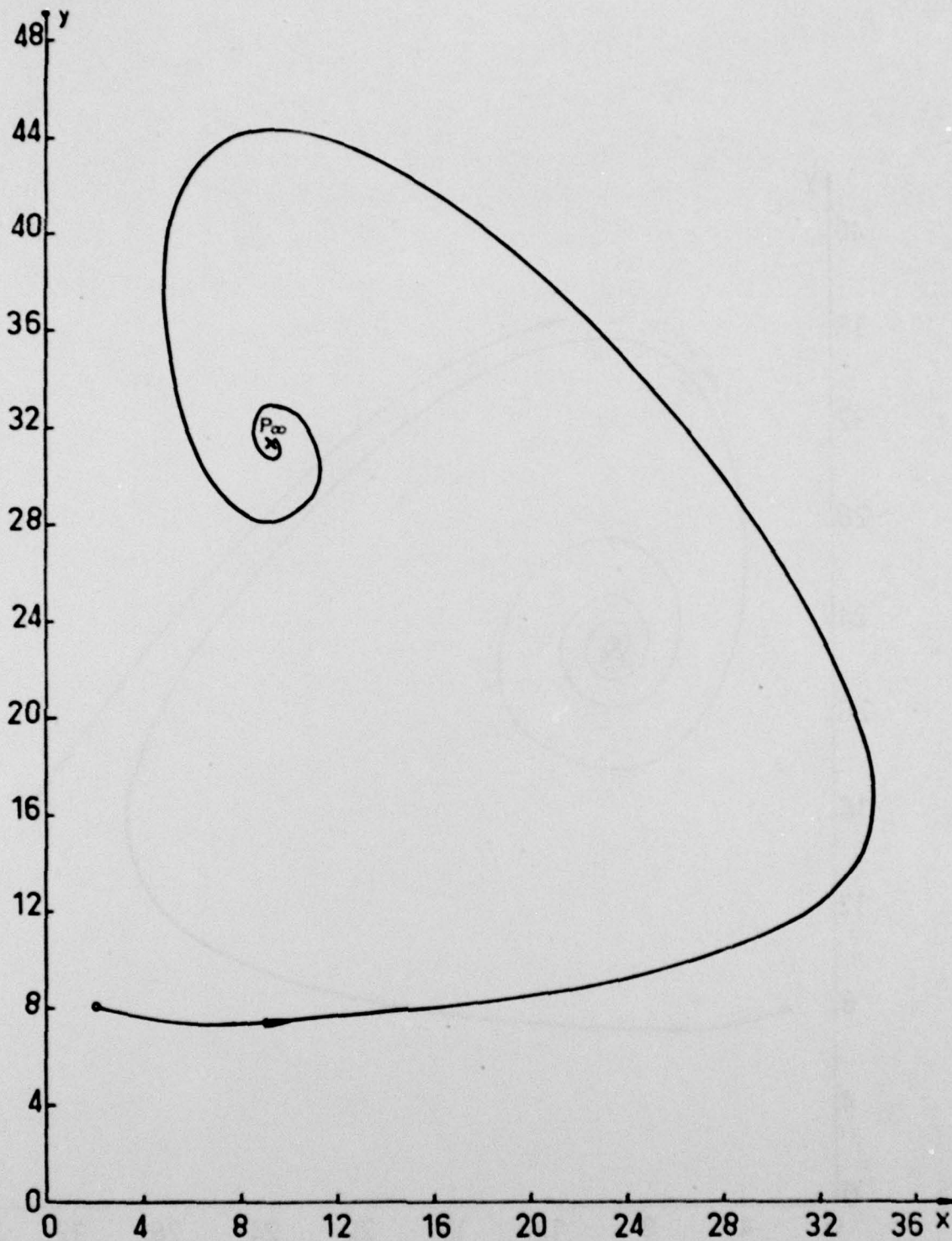
Fig. 15

····to P∞

P∞

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Fig.16

Fig. 17

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7. CONCLUSIONS

It appears that qualitatively the effect of increasing one of the stocking rates while holding the other one fixed is quite similar to the effect under single-species stocking . Predator stocking tends to promote prey extinction, which could have practical applications for a pestilential prey species, provided the predator species either requires prey to survive or is itself not a nuisance. Prey stocking tends to stabilize the system and increase the predator population, which could have practical applications for a predator species which one wishes to harvest in quantity.

If the predator species is a fish and the prey species is its food, our results indicate that indiscriminate fish stocking may exhaust the food supply, leading to a collapse of the fish population. Food supply stocking, possibly coupled with modest fish stocking is a safer and more productive procedure. Computer simulations may be of great use in determining optimal stocking rates, taking into account not only such factors as stability, but also food costs. Our results indicate some directions to be taken in analyzing mixed stocking and harvesting situations, which could have practical significance. We propose to continue with this investigation.

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We examine the qualitative effects of constant-rate stocking of either
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